Neurophysiology: **'Monkey see, monkey do' cells**

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Cells in the premotor cortex of the macaque monkey respond to the sight of specific hand actions made by either the animal itself or the experimenter. What could be the function of such cells?

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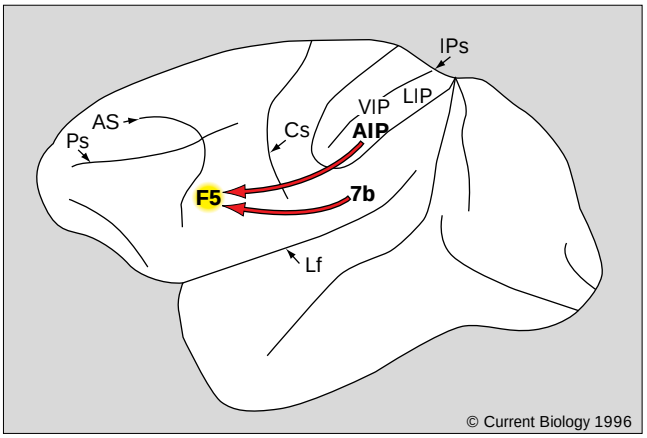
For nearly 40 years, the properties of single neurons in the cerebral cortex of the macaque monkey have been extensively probed and dutifully catalogued. Many characteristics of these cells have been described, such as the remarkable selectivity of units that respond to very specific visual stimuli, such as faces, and responses made by other cells when the monkey prepares a limb or an eye movement. A recent paper by Gallese *et al.* [1] describes a type of cell in the premotor cortex which has properties that are extremely difficult to understand in exclusively sensory or motor terms.

A cell of the type described by Gallese *et al.* [1] increases its firing rate when the monkey views a person grasping a small morsel of food, such as a raisin, or one person grasping a raisin from the hand of another. The cell also responds when the monkey itself grasps the raisin. Is this cell simply interested in raisins? The answer is no, because the neuron does not respond to the sight of the raisin alone. Is this cell simply interested in grasping? Again the answer is no, because it does not respond to the sight of a grasping action in the absence of the raisin. Interestingly, these neurons do not respond when the monkey watches the raisin being grasped with pincers.

Other, similar neurons have been found in the same region of cortex that are selective for different hand–object interactions, such as tearing, holding or placing. Like the responses of the 'grasp-the-raisin' cell described above, the firing rates of these neurons are influenced by the animal's performance of the action as well as its observation of the same action performed by others. These neurons are found in premotor area F5, which is heavily interconnected with two regions in the parietal lobe that are known to play a role in the sensorimotor control of grasping movements (Fig. 1). Gallese *et al.* [1] have described such cells as 'mirror neurons', as they respond to the sight of the monkey itself performing the act, as well as to the sight of an external agent performing the same (or a similar) action. I prefer the more descriptive term 'monkey see, monkey do' neurons, which I first heard used by David Perrett. Either seeing or performing the appropriate act changes the firing rates of these fascinating cells.

In the past, critics of single-cell recording have argued against the usefulness of this sort of enterprise. One argument is that the data can only yield insights into brain function for sensory or motor systems, where cells change their rate of firing in relation to sensory stimuli or movements in ways that seem easy to understand. More complex, cognitive operations in the brain will inevitably escape the grasp of the neurophysiologist, so the argument goes. One version of this position considers the vast majority of cortical neurons to be "hidden units" in a multilayered, connectionist neural network; describing the activity of any single such unit will tell the scientist next to nothing about the properties and function of the whole network [2]. Fortunately, we know much more than just the analog firing patterns of single cells. A great deal is known about the response profiles of a large number of neurons in premotor area F5 and the surrounding frontal cortex [3,4], and about the neurophysiology and neuropsychology of other regions of so-called 'association cortex', which are interconnected with F5 and related premotor and prefrontal cortical fields [4–8]. This accumulated knowledge helps to restrict ideas about the role(s) of mirror neurons.

Figure 1



A side view of a macaque monkey brain. The 'monkey see, monkey do' neurons described in the text are found in premotor cortical area F5. F5 receives its sensory information from two regions in parietal cortex, AIP (anterior intraparietal area) and 7b. AS, arcuate sulcus; Cs, central sulcus; IPs, intraparietal sulcus; Lf, lateral fissure; Ps, principle sulcus; VIP, ventral intraparietal area; LIP, lateral intraparietal area.

One intriguing possibility is that the cells described by Gallese *et al.* [1] have a major role in what psychologists and neuroscientists usually describe as cognition. Although many have been scornful of such suggestions when it comes to single-cell data, it is certainly tempting to describe these types of neuron as 'grasping' or 'tearing' cells in a very abstract sense of the word. That is, they might code for 'grasping' of any sort in the same way that we use the word 'grasp' to describe a multitude of different sensory and motor events. But if this is indeed the case, why would the cells fail to respond to a raisin being grasped with pincers or a grasping movement made without a raisin? Perhaps the appropriate description is a 'grasping-a-small-object' cell. But we have to be careful of falling into the trap of invoking the equivalent of 'grandmother-wearing-a-red-dress-on-a-tuesday' neurons. If indeed the cells code for 'grasping a small object', could it be that mirror neurons simply respond to very specific visual stimuli — such as grasping a raisin or tearing a sheet of paper — in the same way that cells in the temporal cortex can respond selectively to the sight of a specific object such as a hand (and only a hand) or a face (and only a face)? This explanation does not work either; many mirror neurons respond when the animal makes the appropriate movement in complete darkness, so the cells cannot be exclusively visual.

Gallese and colleagues [3,4,9] have argued that mirror neurons play a role in matching movement observations to movement execution. The function of this matching process has yet to be specified. It certainly is not, in any simple sense, for preparing the movement. Electromyographic recordings from the monkey's hand rule out the possibility that the animal actually prepares to make a grasping or tearing movement when it observes a graspable or tearable object, or watches some other agent grasping or tearing. Gallese and colleagues have suggested that the matching system is concerned with the meaning of actions in some abstract sense. And yet, curiously, F5 neurons seem relatively uninterested in other actions that clearly have meaning for the monkey, such as threat gestures, arm waving and so on [3]. Perhaps other premotor or prefrontal fields respond to gestures which are not related to hand–object interactions.

Whatever their exact functions, F5 neurons are part of a circuit which is crucial for the successful visual control of manual actions. Gallese and colleagues [4] have found deficits in visually-guided grasping when F5 neurons are temporally inactivated by localized injections of muscimol. These deficits share a number of features with the grasping deficits seen after similar inactivation of parietal cortex (more specifically, the anterior intraparietal area, AIP, with which F5 is interconnected). The study of the sensorimotor control of grasping has become a rather popular target topic for neuroscientists of every persuasion; perhaps mirror neurons will provide a much-needed intersection for the relevant neurophysiology and neuropsychology.

One of the most exciting developments related to mirror neurons is evidence emerging from functional imaging studies. Gallese and colleagues have postulated that a similar action observation/execution system may exist in human frontal cortex, perhaps in Broca's area (a region typically associated with speech rather than hand function). Activation in Broca's area was indeed observed in a recent study ([3], see also [10]) in which positron emission tomography was used to identify regions of the human brain most active during action observation; other functional imaging studies of visually-guided grasping, however, have not always found increased activity in this region [11,12]. The real promise of this kind of work is that it will address theories of premotor cortex functions, and perhaps even theories of the evolution of language [1,3,9]. For example, many biologists have argued that manual gestures, rather than vocalizations, in a primate ancestor may have been the precurser to language (see [13] for review). Perhaps by increasing our understanding of the 'vocabulary' of mirror neurons we may find ourselves one step closer to understanding a hallmark of our species — speech and language.

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